

LETTER

Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs

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Abstract

Biodiversity is frequently associated with functional redundancy. Indo-Pacific coral reefs incorporate some of the most diverse ecosystems on the globe with over 3000 species of fishes recorded from the region. Despite this diversity, we document changes in ecosystem function on coral reefs at regional biogeographical scales as a result of overfishing of just one species, the giant humphead parrotfish (*Bolbometopon muricatum*). Each parrotfish ingests over 5 tonnes of structural reef carbonates per year, almost half being living corals. On relatively unexploited oceanic reefs, total ingestion rates per m² balance estimated rates of reef growth. However, human activity and ecosystem disruption are strongly correlated, regardless of local fish biodiversity. The results emphasize the need to consider the functional role of species when formulating management strategies and the potential weakness of the link between biodiversity and ecosystem resilience.

Keywords

Biodiversity, bioerosion, coral reefs, ecosystem function, functional redundancy, over fishing, reef fish.

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INTRODUCTION

The global loss of biodiversity and the prospect of ecosystem collapse have focussed our attention on the role that species play in ecosystem processes (McCann 2000; Jackson *et al.* 2001), particularly the relationship between biodiversity and ecosystem function (e.g. Chapin *et al.* 2000; Petchey & Gaston 2002). To date, the vast majority of studies of ecosystem function have concentrated on relatively simple systems, usually at relatively small scales (Naeem & Li 1997; Tilman *et al.* 2001; Paine 2002). From such studies the consensus is that systems with high species richness and functional diversity should be relatively stable and insensitive to perturbations (McCann 2000). Our data challenge this paradigm, with evidence of regional-scale ecosystem disruption in a system characterized by exceptionally high biodiversity and functional complexity: coral reefs.

Coral reefs are shaped by the dynamic interaction between constructional and decompositional processes: calcification by corals and algae vs. erosion by physical and/or biological agents. Here we focus on the latter, bioerosion, which on intact reefs is primarily a result of the

grazing activity of parrotfishes (Hutchings 1986; Bellwood 1995a). By quantifying the activities of parrotfishes – the only fish group that consistently remove carbonate from the reef matrix when feeding – we can accurately quantify a major reef process, bioerosion. Comparing rates of erosion at 44 sites across the Indo-Pacific we demonstrate the impact of human activity on ecosystem function across biogeographical regions and evaluate the potential for functional redundancy in diverse ecosystems.

METHODS

Erosion rates were calculated using bite rates, bite scar volumes and fish abundances. Fish abundances on the Great Barrier Reef (GBR) were estimated based on 132 timed transects (20-min long, 5-m wide) at nine reefs. Timed transects were selected to minimize observer effects and increase encounter rates. Transect lengths were calculated using differential GPS readings at the ends of each transect. We censused four transects per habitat, three to four habitats per reef, and three reefs at each shelf location: inner, middle and outer. Details of census methods and locations are given in Bellwood & Wainwright (2001). Only

adult specimens were included in the analyses to increase census precision and provide conservative erosion estimates. Feeding rates and bite volumes for *Scarus* and *Chlorurus* species were taken from the literature (Bellwood & Choat 1990; Bellwood 1995a). *Bolbometopon muricatum* (Valenciennes) feeding rates were based on 110 min of digital video (DV) recordings of schools on Yonge and Hicks Reefs on the GBR. Individual fish were tracked on DV by recording the bites per second (mean observation time 36.9 s). *Bolbometopon muricatum* bite volumes ($n = 351$) were calculated by following schools and measuring fresh feeding scars. Feeding day-lengths and substratum densities were taken from the literature (Bellwood 1995a). Patterns of prey use and selectivity by *B. muricatum*, were examined by comparing the locations of bite scars ($n = 421$) with substratum cover on 12×30 m line-intercept transects laid haphazardly in *B. muricatum* feeding zones. Selectivity was estimated using Manly's selectivity index (Manly *et al.* 1993).

Regional patterns of erosion were examined based on 44 sites across the Indo-West Pacific (Fig. 1), with four sites each at Cocos (Keeling) Islands, Rowley Shoals (northwest Australia), Togean Islands, Northern Sulawesi (Indonesia), Yonge, Day and Hicks Reefs (GBR), Pohnpei, Kosrae (Micronesia), Tahiti and Moorea (French Polynesia). All censuses were on reefs exposed to the open sea. Species abundances are based on combined censuses from the slope, crest and flat at each site, to allow for any movement of fishes in response to fishing pressure (Johannes 1980). Area was estimated by using the mean distance of a 20-min swim from the GBR data (235 m). A human impact index was estimated based on human population densities on the adjacent land mass ($0.5 \times \text{people km}^{-2}$; Dalzell *et al.* 1996; Edwards 1996). With two exceptions (Rowley Shoals and the GBR) all locations have a strong local tradition of artisanal fishing for reef fishes, with large parrotfishes being a prized and targeted component (Johannes 1980; Dalzell *et al.* 1996). Although the Rowley Shoals and GBR have no

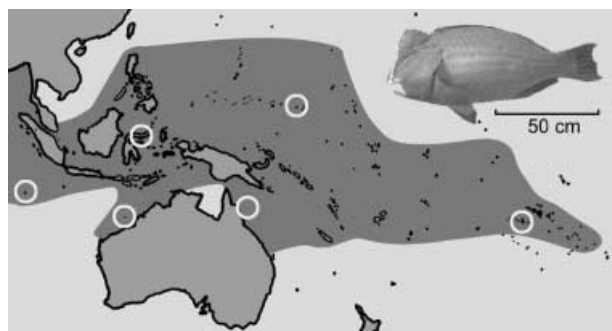


Figure 1 Geographical range of the giant coral eating parrotfish *Bolbometopon muricatum* in the Indo-West Pacific, and the regions examined.

parrotfish fishery, to be conservative, the human impact index was calculated on the same basis as elsewhere.

RESULTS

The GBR has no directed fishery for parrotfishes, and represents a baseline in a system with limited human impact. Here, fish erosion is largely restricted to just two of the 27 parrotfish species (Fig. 2). *Chlorurus microrhinos* (Bleeker) (up to 70 cm total length) is the primary bioeroder on mid-shelf reefs, while *B. muricatum* is by far the largest bioeroder (up to 120 cm total length) and is the major contributor on outershelf reefs, where it regularly occurs in schools of 30–50 individuals. With a mean bite rate of $6.09 \text{ bites min}^{-1}$ ($\pm 0.35 \text{ SE}$) and bite volume of 1.66 cm^3 ($\pm 0.10 \text{ SE}$) each individual *B. muricatum* removes an estimated 2.33 m^3 or 5.69 ($\pm 0.53 \text{ SE}$) tonnes of carbonate each year. Given the mean abundance of this species on the outer reef crest, this equates to $279.3 \text{ tonnes ha}^{-1}$ or 27.9 kg m^{-2} (Fig. 2).

Where significant human impact and fishing pressure exists, the picture is strikingly different (Fig. 3). Using a combination of three reef habitats (flat, crest, slope) to encompass the full range of seaward habitats used by parrotfishes, we find that for almost half of the 44 sites examined there is almost no significant external bioerosion by parrotfishes. Significant erosion was only recorded from reefs protected from human activity (Rowley Shoals and the northern GBR are both Marine Parks in remote locations). The contrast between protected and impacted reefs is striking, with parrotfish erosion and estimated human impact being strongly correlated (Fig. 3). This relationship holds irrespective of geographical location. Low rates were recorded in the

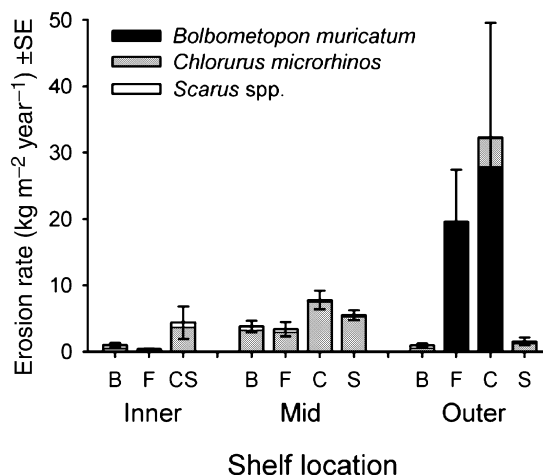


Figure 2 Local variation in bioerosion by parrotfishes across the Great Barrier Reef. The totals incorporate all parrotfish species (28 species) although only two species can be graphically resolved at this scale (the 21 *Scarus* species contribute less than 5% of total erosion). B: backreef, F: reef flat, C: reef crest, S: reef slope.

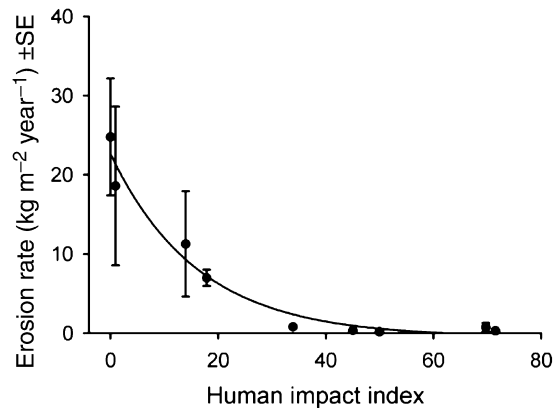


Figure 3 The impact of human activity on ecosystem function, illustrated by total bioerosion rates by parrotfishes (slope, crest and flat habitats combined) vs. a human impact index ($r = 0.98$). The human impact in most locations is primarily mediated through reef fisheries, especially spearfishing and netting (Dalzell et al. 1996). Locations in order of increasing human impact: Rowley Shoals, GBR, Togean Isl, Cocos (Keeling), Kosrae, Moorea, Pohnpei, Northern Sulawesi and Tahiti (each point is a mean \pm SE of four sites at each location).

Indo-Australian Archipelago, the centre of coral reef fish diversity (Bellwood & Hughes 2001) and the centre of the geographical range of *B. muricatum*, and in peripheral locations (Micronesia and Polynesia). Although *B. muricatum* were recorded on isolated offshore reefs in the Togean Islands in central Sulawesi, in seven of the eight Indonesian sites, and in all 16 Micronesian and French Polynesian sites, *B. muricatum* and *Chlorurus* densities were extremely low. This results in extremely low rates of bioerosion by parrotfishes and regional-scale disruption to ecosystem processes.

In addition to bioerosion, *B. muricatum* is also a major coral predator. Unlike *Chlorurus* and *Scarus* species, *B. muricatum* regularly feeds on living corals. On average, 48.2% (± 6.6 SE) of *B. muricatum* bites on GBR reefs were on living scleractinian corals. This equates to $\approx 13.5 \text{ kg m}^{-2} \text{ year}^{-1}$. Bites (coral and non-coral) were invariably from convex surfaces but *B. muricatum* displayed little other evidence of selectivity. Of the six most abundant prey types (in order of decreasing utilization: epilithic algae, coralline algae, *Acropora* 'isopora' group, *Pocillopora verrucosa*, *A. 'humilis'* group, *Montipora* spp. and 'other corals'), only *Montipora* spp. were consistently avoided.

DISCUSSION

Despite supporting over 3000 fish species, only one family, the parrotfishes, consistently removes reef carbonate when feeding. Of the 35 parrotfish species present on the study reefs, almost all erosion on oceanic reefs can be attributed to just one species: *B. muricatum*. It is a major contributor to

reef ecosystem processes and its absence highlights the potential for marked changes in ecosystem function. The impact of this change in parrotfish bioerosion in ecosystem processes is best evaluated by comparison with rates of calcification (i.e. rates of reef growth). Annual calcification on coral reefs is usually estimated to be in the order of 3–10 kg m^{-2} , but may approach 35 kg m^{-2} , with the highest rates on seaward reef crests (Barnes & Chalker 1990). With estimated mean erosion rates of 32.3 $\text{kg m}^{-2} \text{ year}^{-1}$ on the reef crest, parrotfish erosion on the outer GBR reefs approaches these maximum estimated calcification rates. It appears that virtually all bioerosion in this high-production high-erosion crest habitat, is via parrotfishes. This represents the highest erosion rate recorded on coral reefs (Hutchings 1986; Bellwood 1995a; Eakin 1996). Lower erosion rates in other habitats (Fig. 2) likewise match the lower estimated calcification rates. The loss of bioeroding parrotfishes therefore, represents a major phase shift in ecosystem dynamics, from steady-state reef calcification to carbonate accumulation. The long-term consequences are unknown but may be dramatic.

Removing 13.5 kg m^{-2} of live coral per year, *B. muricatum* is also a major coral predator and is likely to influence coral growth rates, mortality rates, colony shape, colony fitness and coral distributions. The almost complete absence of *B. muricatum* from French Polynesia and Micronesia may have profound effects on coral community structure, biogeography and demography. Faced with the loss of a major predator, and a potential keystone species, one would predict significant changes to coral community structure, in particular an increase in fast-growing grazing-resistant forms (*Pocillopora*, tabulate acroporas and *Montipora*). Furthermore, the loss of parrotfish bioerosion would be anticipated to result in structural instability as erosional activity becomes dominated by either physical processes, with periodic disruption caused by storms, or invasive erosion by echinoids which create channels in the reef matrix. The absence of parrotfishes will impair normal recovery processes and constitutes a loss of ecosystem resilience (Nyström et al. 2000; Lyons & Schwartz 2001).

The influence of *B. muricatum* on coral reefs is qualitatively different from other forms of reef disturbance, such as storms or cyclones (Connell et al. 1997; Nyström & Folke 2000), as the impact is highly consistent, not periodic. Moreover, the redistribution of 32.3 $\text{kg m}^{-2} \text{ year}^{-1}$ of structural carbonates as sediments will have a marked influence on the habitat structure of adjacent areas. Bioerosion by parrotfishes contributes directly to both the loss of carbonates from reef structures and the creation of adjacent sediment aprons (Bellwood 1995b).

The potential for the replacement of parrotfishes by other functional groups is limited. They are the only group of fishes to consume structural reef carbonates. Echinoids are

functional replacements only in that they remove carbonate. The nature of this erosion is markedly different (they are not restricted to convexities) and in large numbers their activities can be highly detrimental (Eakin 1996). Increasing echinoid numbers are widely regarded as a negative consequence of overfishing (McClanahan & Shafir 1990; Hughes 1994). Indeed, the prevalence of echinoids in marginal reef systems may reflect an enhanced vulnerability to ecosystem disruption in these systems (Hughes 1994; Eakin 1996; Bellwood & Hughes 2001). Furthermore, bioeroding parrotfishes are unlikely to respond to current conservation strategies. *Chlorurus* species and *B. muricatum* both cover large areas, either when foraging or at dusk (Bellwood 1995a), and *B. muricatum*, in particular, is highly susceptible to spearfishing activity (Johannes 1980; Dalzell *et al.* 1996). Given the small size of most marine protected areas in heavily fished regions it is not surprising that reserves show little positive effects on parrotfish abundances (Russ & Alcala 1998).

If coral reefs are the world's canary, our global early warning system (O'Neill & Oppenheimer 2002), then the fate of parrotfishes is a critical issue. Bioerosion by parrotfishes is a major process in Indo-Pacific coral reef ecosystems, with erosion rates often matching maximum estimated calcification rates. Even without the impacts of global warming, human activity has already decimated these bioeroding species and in numerous areas we see the potential for a major disruption to reef ecosystem processes. The sobering fact is that despite high biodiversity on coral reefs, with over 3000 fish species, a major ecosystem process may be shaped by the activities of just one species. This emphasizes the vulnerability of ecosystem processes and highlights the need to consider both species and functional roles when establishing conservation priorities (Purvis & Hector 2000; Paine 2002; Vanni *et al.* 2002). Protecting biodiversity and regional hotspots is only a first step (Hughes *et al.* 2002). The challenge is to look beyond biodiversity so that we may identify and protect key functional elements in marine ecosystems.

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REFERENCES

- Barnes, D.J. & Chalker, B.E. (1990). Calcification and photosynthesis in reef-building corals and algae. In: *Coral Reefs. Ecosystems of the World*, Vol. 25 (ed. Dubinsky, Z.). Elsevier, Amsterdam, pp. 109–131.
- Bellwood, D.R. (1995a). Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Mar. Biol.*, 121, 419–429.
- Bellwood, D.R. (1995b). Carbonate transport and within reef patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 117, 127–136.
- Bellwood, D.R. & Choat, J.H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Env. Biol. Fishes*, 28, 189–214.
- Bellwood, D.R. & Hughes, T.P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, 292, 1532–1534.
- Bellwood, D.R. & Wainwright, P.C. (2001). Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs*, 20, 139–150.
- Chapin, F.S.I., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L. *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.
- Connell, J.H., Hughes, T.P. & Wallace, C.C. (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.*, 67, 461–488.
- Dalzell, P., Adams, T.J.H. & Polunin, N.V.C. (1996). Coastal fisheries in the Pacific Islands. *Oceanogr. Mar. Biol. Ann. Rev.*, 34, 395–531.
- Eakin, C.M. (1996). Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs*, 15, 109–119.
- Edwards, G.M. (1996). *Britanica World Data. Britanica Book of the Year*. Encyclopedia Britanica, Chicago, IL.
- Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002). Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecol. Lett.*, 5, 775–784.
- Hutchings, P.A. (1986). Biological destruction of coral reefs. *Coral Reefs*, 4, 239–252.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–638.
- Johannes, R.E. (1980). *Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia*. University of California Press, Berkeley, CA.
- Lyons, K.G. & Schwartz, M.W. (2001). Rare species loss alters ecosystem function – invasion resistance. *Ecol. Lett.*, 4, 358–365.
- Manly, B.F.J., McDonald, L.L. & Thomas, D.L. (1993). *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman and Hall, London.
- McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.
- McClanahan, T.R. & Shafir, S.H. (1990). Causes and consequences of sea-urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia*, 83, 362–370.
- Naeem, S. & Li, S.B. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507–509.
- Nyström, M., Folke, C. & Moberg, F. (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.*, 15, 413–417.

- Nyström, M. & Folke, C. (2001). Spatial resilience of coral reefs. *Ecosystems*, 4, 406–417.
- O'Neill, B.C. & Oppenheimer, M. (2002). Dangerous climate impacts and the Kyoto protocol. *Science*, 296, 1971–1972.
- Paine, R.T. (2002). Trophic control of production in a rocky intertidal community. *Science*, 296, 736–739.
- Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.
- Purvis, A. & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405, 212–219.
- Russ, G.R. & Alcala, A.C. (1998). Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs*, 17, 399–416.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.
- Vanni, M.J., Flecker, A.S., Hood, J.M., & Headworth J.L. (2002). Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecol. Lett.*, 5, 285–293.

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